

The University of Chicago

ONTOGENY OF THE LEAF AND
INDUSIUM IN PTERIS
AND PTERIDIUM

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY
AUGUST, 1941

By
CARLOS RAFAEL GARCIA

CHICAGO, ILLINOIS

1944

The University of Chicago

ONTOGENY OF THE LEAF AND
INDUSIUM IN PTERIS
AND PTERIDIUM

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

AUGUST, 1941

By

CARLOS RAFAEL GARCIA

CHICAGO, ILLINOIS

1944



ONTOGENY OF THE LEAF AND INDUSIUM IN PTERIS AND PTERIDIUM

Introduction

The taxonomic status of the genera Pteris and Pteridium has always been a matter of great uncertainty and discussion. The characteristics for both of these genera are so similar that many times a single genus, the genus Pteris, has included the Pteridiums as well. The difficulty arises mainly from an insufficient knowledge of the soral characters of both genera. This, however, is not at all surprising when the inconstancy of the critical characters in the genus Pteridium is taken into account. According to Tryon (8), such critical characters as the ciliation of the indusium, the pubescence on the underside of the blade, and others, are so inconstant that it has led to the creation of a large number of species in the genus Pteridium, when in reality the differences seem to be mainly attributable to ecological factors and therefore, not significant enough to justify the great number of species, although of sufficient importance to validate the creation of varieties within the species. According to this new revision of Pteridium (8) there is a single species, P. aquilinum, with two subspecies, typicum and caudatum, each with their corresponding number of varieties, seven for typicum and three for caudatum.

The rôle of the indusium in this new classification is very important and it is the principal aim of this investigation to trace the origin and development of such a structure in several varieties. Bower (3) illustrates one of the stages of this development by means of a figure taken from Luerksen (7). The original figure is credited to Burck (4) but his work has not been available for study. This is the only citation available in the literature with reference to the stages of indusial development in Pteridium.

Materials and Method

The Pteridium material examined for this investigation was collected at four different localities. The variety latiusculum was collected at the Dune region near Gary, Indiana; the variety pubescens was collected at Walla Walla County, Washington, and at Kooskooskie, Oregon; and the variety arachnoideum at Las Cruces, Puerto Rico.

Pteris longifolia leaves were collected at the Greenhouses of the University of Chicago.

The collections included very young leaves before they start unfolding, different stages in the veneration of the leaves, and quite mature leaves. The material was mainly killed and fixed in a formalin-acetic-alcohol mixture (Kraus' Formula). Some was killed and fixed in Navaschin's solution (Crooks' Modification). It was all prepared to be sectioned in paraffin by the tertiary-butyl-alcohol method, and sectioned at ten microns. Some of the sections were stained in the usual triple stain combination and others in safranin and fast green. Drawings of the principal stages of the development of the leaf and the indusium were made with the aid of a camera lucida.

Results and Discussion

Pteridium

The Pteridiums possess a deep-seated rhizome from which branches appear, and at the branches nearest the soil surface, the leaves are born. There is a dormant bud at the base of each leaf and from this dormant bud the leaves for the succeeding year develop. The rhizome has a distinct dorsiventral arrangement, and the tip is densely covered with hairs which protect the peculiar lens-shaped apical cell with two cutting surfaces (5) that is responsible for the growth of the rhizome.

The Leaf

When very young, the petiole (stipe) is the most prominent part of the leaf, with a tip which bends downward rather abruptly forming a small hook-shaped structure resembling a crochet-hook. From this hook-shaped portion the blade develops. This growing tip is densely covered with hairs which during later stages of de-

velopment disappear almost completely. The pinnae arise as lateral outgrowths from the rachis portion of the leaf, and when still very young, pinnules originate lateral to the pinnae. Formation of new cells and determination of leaf topography of the pinnae and pinnules is controlled by a three-sided apical cell which is present at the tips of both structures (fig. 8).

The margin of the pinnules consists of a row of wedge-shaped cells, oriented so that the rectangular aspect is seen on and beneath the surface (fig. 11) and the triangular aspect in the cross section of the pinnule (fig. 1). In their triangular aspect, these initials much resemble apical cells (fig. 1), even dividing so that each new cell wall is parallel to the uppermost or the lowermost surface of the wedge-shaped cells (an iso-prismatic division). These new cells, the segments, divide periclinally and anticlinally forming additional cells which together with the marginal row develop into the pinnule (figs. 1,2,3,4). The size and the number of cells on the adaxial surface of the pinnules is greater than that on the abaxial and thus the developing pinnules are curved on both their sides to make an incomplete coil. As development proceeds, the pinnules straighten out almost completely with the exception of the marginal portion which remains incurved. It is from this incurved region that soral development occurs if the leaf is a fertile one. If sterile, the margin is also incurved but no other structures develop from it. Both the upper and the lower surfaces of the blade may develop hairs, the amount and occurrence of these depending upon the variety involved.

The Indusium

The term "indusium" is one of the most indefinite terms used in pteridology. According to Bower (1), "the term 'indusium' has been applied to bodies of the most various form, position and structure, born in relation to the Fern-sorus and serving for the protection of the sporangia." Bower (1,2) defines the indusium as "an inconstant body, varying in occurrence, and in position," and uses the term "to designate outgrowths protective of the sorus, whatever their position and whatever their evolutionary history may have been."

This definition tends to emphasize the function of the structure rather than the structure itself. Accordingly, as Bower

(1,2) suggests, Pteridium has only one indusium, and that is the one formed by the specialized margin of the blade which actually curves around the receptacle and gives protection to the developing sporangia. The inner indusium in Pteridium, according to such a definition, would no longer be considered an indusium since its protective character can at no time be definitely established.

If the morphological aspect of the definition is emphasized, then Pteridium possesses two indusia, an outer and an inner one. The outer indusium is the one formed by the specialized margin of the leaf, and it is a persistent membranous flap which develops in connection with the receptacle and offers adequate protection to the developing sporangia (fig. 13). The inner indusium is initiated on the proximal side of the region which will form the receptacle. It is a small membranous outgrowth which starts from an epidermal cell and whose development may vary considerably (figs. 5,6,7). In most of the pinnules studied it appears as a rudimentary or vestigial membrane or as series of simple hairs and may be continuous or in certain areas may be completely lacking. The inner indusium is usually evident during the early phases of receptacle development (figs. 9,10,12), but once the latter is fully differentiated and the sporangium initials are clearly set off, it is no longer clearly detectable (fig. 13). It probably dries out and becomes detached from the plant.

The outer indusium develops from the row of wedge-shaped initials at the margins of the pinnules. After these initials fully establish the blade portion of the pinnules, each one of these wedge-shaped cells, as seen in cross section, undergoes a transverse division (chordal division) forming two cells. The distal (outermost) one is dome-shaped and the proximal (innermost) is triangular (figs. 5,6). The dome-shaped cell continues to divide transversely to give rise to the marginal membranous flap, which when formed in connection with the receptacle is known as the outer indusium. Sterile blades develop the same type of specialized pinnule margin. The triangular cell may undergo a few divisions radially and transversely and contribute some to the formation of the marginal flap.

The inner indusium is never as definite a structure as the outer one is (figs. 9,10,12,13). The reduction in the number of cells and the discontinuous nature of most inner indusia in Pteridium indicate that such a structure is rudimentary and in the

course of disappearing from the genus.

The Receptacle

Epidermal cells between the base of the outer indusium and the inner indusium continue to be meristematic (figs. 5,6,7). As a result, a mass of tissue develops, the receptacle, from which the sporangium initials differentiate. By this time the inner indusium has almost always disappeared and the outer indusium has grown and incurved to such an extent that it often completely covers the developing receptacle (fig. 13). At a rather young stage in the development of the receptacle (fig. 12) cells in the blade immediately beneath the developing structure, start to differentiate into vascular tissue and will later form a vein commissure to the ends of the lateral veins of the pinnules. In this way the receptacle is provided with a vascular system.

Comparison with Leaf and Indusium Development in *Pteris*

The development of the leaf and the indusium of *Pteris longifolia* has been described previously by García (6). The leaf ontogeny of *Pteris* and *Pteridium* is very similar. Formation and expansion of the blade in both genera is controlled by a row of wedge-shaped marginal cells on each side of the developing pinnae or pinnules. These marginal cells give rise to the incurved margin which forms the indusion of *Pteris*. Indusium development in *Pteridium* is the same as in the genus *Pteris* and the incurved margin constitutes the outer indusium. *Pteris* shows no indication whatsoever of even a vestigial inner indusium such as is found in *Pteridium*. The receptacle in *Pteridium* is a more massive and definite structure than in *Pteris*, and develops to a considerable size before the appearance of sporangium initials. In *Pteris* the receptacle is not as evident and the sporangium initials develop directly from specialized epidermal cells.

The presence of this vestigial inner indusium places the genus *Pteridium* in a more primitive position with reference to the genus *Pteris*. The fact that the inner indusium is so inconstant and that the leaf and indusium development in both genera is so strikingly similar indicates that they are rather closely related. This may account for the older interpretations where ferns with

or without an inner indusium but possessing other similarities were included in a single genus, Pteris. On the basis of recent taxonomic studies (8) and the ontogenetic studies reported here, sufficient criteria exist to differentiate Pteris and Pteridium as valid genera.

Summary and Conclusions

1. The developing leaf blade of Pteridium, in its early stages, is a hook-shaped structure densely covered with hairs, occurring on the tip of the prominent petiole (stipe).

2. The formation and expansion of the blade is controlled by a marginal row of wedge-shaped initials occurring on both sides of the pinnules.

3. The wedge-shaped initials form new cells iso-prismatically by means of divisions parallel to the two cutting surfaces. The resulting segments divide periclinally and anticlinally and together with the marginal row of initials form the pinnule.

4. The size and the number of cells is greater on the ad-axial surface of the developing pinnules than on the abaxial, so that in early stages of development the pinnule is nearly completely incurved and appears coiled in cross section. Later it straightens out horizontally except for the margin which always remains incurved and will later differentiate into the outer indisium.

5. The outer indusium, as seen in cross section, arises from the wedge-shaped initials when a vertical transverse division (a chordal division) of each cell gives rise to an outer dome-shaped derivative and an inner more or less triangular cell. The outer cell divides transversely to form the long membranous flap which constitutes the outer indusium. The inner cell may divide thus contributing some cells to the outer indusium.

6. The inner indusium is a vestigial or rudimentary structure of a rather indefinite and inconstant character which develops from the epidermal cell proximal to the receptacle. It starts its development when the receptacle is very young and incompletely differentiated. The inner indusium may form a continuous membrane, an irregularly broken one or simply consist of a few hairs. In most leaves examined this structure is vestigial and nearly obsolete.

7. The receptacle develops at the base of the incurved margin between the outer indusium and the inner indusium. In the ab-

sence of an inner indusium it develops comparably, proximal to the outer indusium. The receptacle is highly meristematic and at the time of sporangium initiation is a rather massive structure.

8. When the receptacle is still meristematic, a group of cells in the pinnule near the base of the receptacle differentiates into a vein which connects the terminal portions of the lateral veins of the pinnule and supplies the developing sorus with a vascular system.

9. The number of occurrence of hairs on the leaf and indusia of Pteridium varies according to the variety and may be associated with the habitat of the plant.

10. The leaf development in Pteridium is very similar to that of Pteris. The outer indusium of Pteridium develops in the same way as that of Pteris. There is no inner indusium, nor vestige of one, in Pteris.

11. Pteridium, because of its inner indusium, which often is vestigial, is a more primitive genus than Pteris.

ACKNOWLEDGMENT

Sincere appreciation is expressed to Dr. Paul D. Voth for his interest and helpful suggestions during the preparation of this work.

Literature Cited

1. Bower, F. O., Studies in the morphology of spore-producing members.--No. IV The Leptosporangiate Ferns. Philosophical Transactions of the Royal Society of London. Series B. 192: 29-138. 1900.
2. Bower, F. O., The Ferns (Filicales) Vol. I, Pp. 359. Cambridge, 1923. (p. 234).
3. Bower, F. O., The Ferns (Filicales) Vol. III, Pp. 306. Cambridge, 1923. (p. 43).
4. Burck, Indusium der Varenis. Inaug. Diss. (Haarlem?) 1874. (Not seen by author).
5. Chang, C. Y., Origin and development of tissues in rhizome of Pteris aquilina. Bot. Gaz. 83: 288-306, 1927.
6. García, C. R., Ontogeny of the frond of Pteris longifolia L., Unpublished Master's thesis, Department of Botany, University of Chicago, 1939. Pp. 13.
7. Luerssen, Christian, Die Farnpflanzen. In: Rabenhorst, L. Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz. Second edition. Vol. III, Pp. 906, 1889 (p. 101, fig. 81).
8. Tryon, Jr., R. M., A revision of the genus Pteridium. Rhodora 43: 1-31; 37-67, 1941.

PLATE I

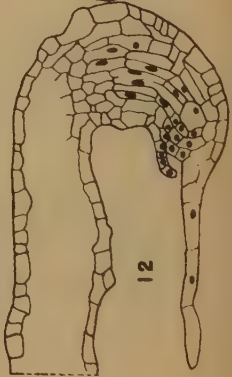
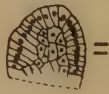
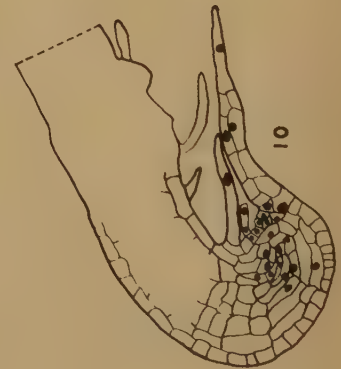
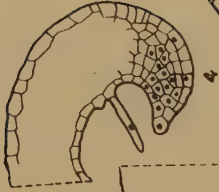
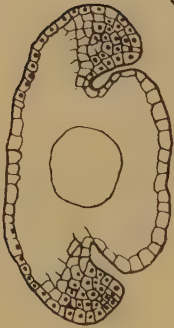
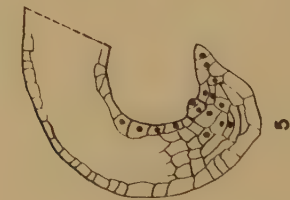


PLATE I

Figs. 1-4--Cross sections of young pinnules at different stages of development. Wedge-shaped initials at the margins, some showing iso-prismatic division.

Figs. 5-7--Cross sections of young pinnules showing the origin of the inner indusium and different stages in the formation of the outer indusium. Chordal division of marginal wedge-shaped initial at fig. 6. Receptacle forming as shown by the increased meristematic activity between the inner and outer indusia.

Fig. 8--Longitudinal section of the tip of a developing leaf showing apical cell.

Figs. 9,10,12--Cross sections of pinnules showing later stages in the development of the inner and outer indusia and the receptacle.

Fig. 11--Surface view of a young pinnule showing the wedge-shaped initials in their rectangular aspect.

Fig. 13--A well developed receptacle from which sporangia are arising. Inner indusium less conspicuous. In many similar sections it was lacking.

